

Thesis/
Reports
Sala, A.

FIRE SUPPRESSION IN PONDEROSA PINE/
DOUGLAS-FIR ECOSYSTEMS CAUSES SHIFTS IN
SOIL RESOURCE AVAILABILITY

Fire suppression in ponderosa pine/Douglas-fir ecosystems causes shifts in soil resource availability

Joint Venture Agreement between the USDA Forest Service Rocky Mountain Research Station
research work unit number ALWRI-4901 and The University of Montana

Principal Investigators:

Anna Sala. Division of Biological Sciences. The University of Montana. Missoula.
Thomas H. DeLuca. Department of Ecosystem and Conservation Science. The University
of Montana. Missoula.

USDA Forest Service Coordinator:

Carol Miller. Aldo Leopold Wilderness Research Institute. Missoula. Montana.

Final Report September 2004

National FS Library
USDA Forest Service

MAY 23 2008

240 W Prospect Rd
Fort Collins CO 80526

Abstract

Since the early 1900's fire exclusion and livestock grazing in the interior northwest have resulted in a successional replacement of open ponderosa pine (*Pinus ponderosa*) stands to dense stands of interior Douglas-fir (*Pseudotsuga menziesii* var *glauca*). However, we little is known on whether and how natural periodical fires influence nitrogen cycle in ponderosa pine systems of the interior northwest and on the long-term effects of fire exclusion on fundamental ecological processes such as changes in species composition and feedbacks on water, nutrient and carbon cycles. Here, we established a series of unmanaged, natural stands in wilderness areas of Northern Idaho subjected to different fire regimes (from no fire for the past 120 years up to four fires) and studied changes in overstory and understory characteristics and associated changes in forest floor and mineral soil properties related to nitrogen cycling from fire maintained to fire excluded stands. Based on fire atlas information, we identified seven sites in the Selway Bitterroot and Gospel Hump wilderness areas, each with at least one stand not burned for the past 80 years (fire excluded) and at least one burned twice or more times (fire maintained). Regardless of fire regime, all stands sampled had a significant old growth living component suggesting that they had not been subjected to stand-replacing fires. While total-stand level basal area did not differ between fire maintained and fire excluded stands, total tree density was higher in fire excluded stands than in fire maintained stands. Such increase in density was due only to the increase in shade tolerant species (mainly Douglas-fir). Grass cover was slightly but significantly greater in fire maintained stands while shrub cover did not differ between the two fire regimes. Forest floor depth and N content increased significantly in fire excluded stands suggesting an accumulation of non labile-N in the litter in these stands. While nitrate and ammonium pools in the mineral soil during June 2003 were not different between fire excluded and fire maintained stands, potentially mineralizable nitrogen and total N content were significantly lower in fire maintained stands. However, net nitrification and nitrifier activity were significantly higher in fire maintained stands. These results suggest that although the total N pool is lower in fire maintained stands, the actual pool of mineralizable N increases in stands subjected to repeated fire relative to excluded stands. To our knowledge this is the first study that compares natural, relatively unmanaged fire excluded and fire maintained stands. Our results generally corroborate the prediction that fire exclusion results in significant changes in forest structure and results in decreases in nitrogen availability.

Introduction

Pure and mixed ponderosa pine (*Pinus ponderosa*) stands cover about 16 million hectares in the western United States (Van Hooser and Keegan 1988). In drier areas of the western United States, ponderosa pine is the potential climax forest type, while in the Cascade and Sierra Nevada ranges and in the Rocky Mountains, this species is seral to more shade tolerant trees such as Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), white fir (*Abies concolor*) and incense cedar (*Calocedrus decurens*). Prior to 1900 most ponderosa pine-dominated stands experienced surface fires at intervals ranging from 10 to 25 years (Stokes and Dieterich 1980; Martin 1982), although longer fire intervals are not uncommon (e.g. Brown et al. 1999; Veblen et al. 2000). Periodical fires thinned out patches of the fire-intolerant, shade-tolerant species and helped maintain open, park-like ponderosa pine stands (Arno 1988; Keane et al. 1989, 1996).

Since the early 1900's fire exclusion and livestock grazing in the interior northwest have resulted in a successional replacement of open ponderosa pine (*Pinus ponderosa*) stands to dense stands of interior Douglas-fir (*Pseudotsuga menziesii* var *glauca*) (Arno et al. 1995). However, we currently have surprisingly little understanding of the long-term effects of fire suppression on fundamental ecological processes such as changes in species composition and feedbacks on water, nutrient and carbon cycles. In the southwestern United States postsettlement forest structure is characterized by very high tree density, dramatic reductions of grassy openings and increases in shrub cover (e.g. Covington and Moore 1994; Covington et al. 1997; Fulé et al. 1997; Feeney et al. 1998; Kaye and Hart 1998; Stone et al. 1999). Within managed areas of the interior Northwest MacKenzie et al. (*in press*) also showed increases in stand basal area with increases in time since the last fire due to the increase of the more shade tolerant and fire sensitive Douglas fir. Concurrent with changes in basal area, there was a progressive increase in total shrub cover in the understory (MacKenzie et al. *in press*). These successional vegetation changes have profound ecological and management implications, including fuel buildup, increase of high-intensity wild fires (Fischer and Bradley 1987) and increase in epidemics (Anderson et al. 1987; Weber and Schweingruber 1995).

Increased tree density and higher LAI in fire-excluded stands is predicted to result in an increase in stand-level transpiration and in intercepted water and snow. The later may be accompanied with a decrease of snow pack accumulation and an increase in evaporation of intercepted water. As a result of these changes, water loss to the atmosphere is predicted to increase and overall surface soil water availability decrease (Feeney et al. 1998; Stone et al. 1999). Increases of water loss to the atmosphere and reduced water availability in the soil may further contribute to desiccation of fuels thus exacerbating the risk of severe wildfires.

Ponderosa pine and Douglas-fir forests of the inland northwest commonly accumulate little inorganic N in the mineral soil because of the slow decay rates and rapid N uptake by plants and microorganisms. Overall, western ponderosa pine forests are considered to be nitrogen limited due to suboptimal levels of available N (Wagle and Kitchen 1972; Mandzak and Moore 1994). This N limitation is thought to be due to the accumulation of organic matter composed of low N woody residues. The exclusion of fire from these forests is assumed to cause stagnant nitrogen cycling and exacerbate the nitrogen limitation in ponderosa pine systems (Covington and Sackett 1984), though this hypothesis is largely untested.

Several mechanisms may account for the increased nitrogen limitation in fire-excluded stands. First, litter quantity and quality have been shown to change significantly with time since last fire as amount of pine and Douglas-fir litter increase in denser, fire excluded stands and as shifts towards slow growing, stress tolerant plants occur in the understory (Mackenzie et al. *in press*). Nutrients may be sequestered in progressively higher amounts of lower quality litter (Hunt et al. 1988; Covington and Sackett 1992; MacKenzie et al. *in press*), which may contribute to nutrient limitations. Second, Newland and DeLuca (2000) found significantly lower abundance of N fixing plant species (mostly herbaceous legumes) in sites with no fire over the last century compared to those recently exposed to prescribed fire or wildfire. Sites regularly opened by harvest prior to reintroduction of fire had the greatest abundance of N fixing plants. Herbaceous legumes provide these sites with a very high N low C substrate. Third, decreases in soil temperature (Kaye and Hart 1998; Covington et al. 1997) and water availability in fire suppressed stands may contribute further to slow down litter decomposition, mineralization and overall nitrogen cycling.

Most of what we know about the consequences of fire exclusion in ponderosa pine ecosystems is derived from either reconstruction of past vegetation based on current conditions in fire excluded forests (e.g. Arno et al. 1995; Fulé et al. 1997), from analyses of changes of vegetation and soil properties with time since last fire (Mackenzie et al. *in press*), or from reversal of conditions after prescribed or wild fire in fire suppressed stands (e.g. Feeney et al. 1998; Stone et al. 1999; Wallin et al. 2004). However, management practices to reverse the effects of fire exclusion in ponderosa pine systems and reset them back to pre-settlement conditions necessarily require the knowledge of the effects of frequent natural fire on these systems and the changes that occur when fire is excluded. Such type of information is virtually non-existent. This may reflect, in part, the challenge to establish reference natural stands affected by repeated natural fires. While studies on changes in forest structure and soil properties with increasing time since fire are very useful to understand successional processes, they provide no information on the effects of frequent, low intensity fires on these properties. Similarly, conclusions derived from reversal of ecological properties after wildfire or the application of prescribed fire in fire excluded stands may be misleading because of 'memory effects' in fire excluded stands where potential shifts in soil resource availability and ecosystem function may have occurred and may not be easily reversed after the application of prescribed fire. While it is frequently assumed that fire exclusion in western low elevation coniferous forests reduces nitrogen turnover, this hypothesis remains largely untested. No study to date has demonstrated that frequent, low intensity fire in ponderosa pine systems increases nitrogen availability. On the contrary, studies on repeated prescribed fire have shown reductions, not increases, in nitrogen availability (Wright and Hart 1997).

The purpose of this study is to identify and fully characterize a set of natural, unmanaged ponderosa pine/Douglas-fir stands in western Montana-northern Idaho wilderness areas at varying stages of fire-exclusion (from fire excluded to fire maintained) and examine changes in stand structure and soil properties. The work reported here is part of a larger ongoing study funded by the USDA-NRI competitive grant program to A. Sala and T. DeLuca to examine the long-term effects of fire exclusion on water availability and N dynamics in ponderosa pine-Douglas fir systems of the interior Northwest. Here, we tested whether frequent fire in unmanaged lower elevation ponderosa pine forests of the interior northwest maintains lower tree density, higher grass cover and lower shrub cover in the understory relative to fire excluded stands. We also examined changes in depth and total C and N content of the forest floor in fire

maintained stands relative to fire excluded stands. In the mineral soil, we tested for differences in base cations, pH, potential mineralizable nitrogen (PMN), total C, total N, NH_4^+ and NO_3^- pool sizes, net mineralization and nitrification, and nitrifier activity between fire maintained and fire excluded stands.

Methods

Location of sites and stands

During the fall 02 and Spring 03, scientists at the Aldo Leopold Wilderness Research Institute compiled a GIS data base superimposing topography, potential vegetation, roads and trails and available digital fire atlases for the Selway Bitterroot Wilderness Area and the Frank Church Wilderness (including the Gospel Hump). Based on this initial data base we selected a series of potential sampling sites. The criteria for site selection included sites with Douglas-fir and ponderosa pine as potential vegetation, slope less than 30%, within 5 miles of the Wilderness boundary and within 1 km of the nearest trail. Based on these criteria, sites were further selected to comprise at least two or three forest stands subjected to different fire histories within the same watershed or small geographic unit:

- a) sites not burned at least since 1900
- b) sites burned once between 1900 and 1930
- c) sites burned twice with the first fire between 1900 and 1930 and the second time between 1930 and 1970, and
- d) sites burned three or more times: the first two during the same intervals as sites burned twice, and the most recent ones after 1970 but prior to 2000.

While fire atlases provided an extensive data base, site accessibility and the relatively narrow criteria imposed (potential vegetation, slopes, and clusters of stands with different fire history within a site) limited site availability. Therefore, we were forced to relax our criteria while maintaining our central objective of selecting sites with clusters of Douglas-fir/ponderosa pine stands that had experienced different fire history, with one stand not burned since 1900, and at least one stand burned twice.

Field reconnaissance and sampling took place during the summer of 2003. During the initial field reconnaissance prior to final sampling, we first identified the different fire history stands within each selected site based on the fire atlas map, GPS coordinates and visual reconnaissance based on presence of charcoal and fire scarred trees (or the lack of them for unburned stands). We noted presence or absence of charcoal and charred trees and, for those stands that had experienced fires, we located and visually inspected fire scarred trees to tentatively count number of lobes on the scars. We also took cores on the fire scars to coarsely corroborate the fire history from the fire atlas once in the lab. In general, based on an approximate visual inspection of the tree fire scars and fire scar cores, fire history was consistent to that in the GIS layers. From this initial field reconnaissance a total of 7 sites were selected for future sampling, each with 2 to 4 stands of varying fire history (Table 1; Figure 1). For simplicity we refer to stands that had not experienced fire during the past 84 to 120 years as fire excluded. The term exclusion, however, refers to both human-induced exclusion and natural lack of fire (i.e. a fire excluded stand in this study may not have necessarily been actively excluded from fire, but rather it may have not had fire to stochastic reasons).

Vegetation Sampling

For each stand, we distributed three, 400 m² plots (20 x 20 m) at approximately equal intervals along the longest distance of central portion the stand to prevent errors in the delineation of the fire perimeters in the fire atlas. Within each stand, plots were no less than 200 m apart. Within each plot, we noted the DBH of all trees greater than 5 cm in diameter by species as well as the number of seedlings by species. Understory vegetation sampling was conducted along two 20 m transects perpendicular to each other which dissected the plot in 4 quarters. Along each transect, we recorded all plants intercepting (or projecting on) the line transect at every 20 cm. Plants intercepting the line transect were recorded by functional groups: grasses and graminoids, forbs, deciduous shrubs, evergreen shrubs and trees. We also distinguished weeds, nitrogen fixing species and, within the evergreen shrubs, ericaceous shrubs. Plants were also categorized in height groups: > 3 m tall, between 0.5 and 3 m and < 0.5 m tall. Whenever possible, plants were identified by species. However, many plants were not flowering and because specimens cannot be collected in wilderness areas we could not identify them. For each plot, we also took DBH and cores from the largest ponderosa pine and Douglas fir within each plot (when available) to later determine the age of the oldest trees.

Soil sampling and chemical analyses

During the summer of 2003, a total of four forest floor and mineral (0-10 cm) soil samples were taken per plot, each consisting of a composite sample from four subsamples taken at each corner of each plot. Soil sampling took place during the last day on each field trip and samples were kept refrigerated in ice until processing in the laboratory.

The forest floor material was oven dried at 70°C and weighed and ground to pass a 200-mesh sieve and analyzed for total C and total N by dry combustion (Fissions EA 1100 Milan Italy). Mineral soil samples were split into two parts, with one being placed in a cold temperature chamber at 5°C for fresh analyses and the second being air dried for storage and dry analyses. Thirty grams of fresh soil was placed into French square bottles with 50 ml of 2 M KCl, the suspension shaken for 30 minutes, and then filtered through Whatman # 2 filter papers. The filtrates were then analyzed for exchangeable NO₃⁻ and NH₄⁺ by using a Autoanalyzer III (Bran Luebbe, Chicago, IL). The salicilate-nitroprusside method was employed for NH₄⁺ and the cadmium reduction method for NO₃⁻ analysis (Mulvaney, 1996). Soils were also analyzed for potentially mineralizable N (PMN) using a 14 d anaerobic incubation procedure. Ten ml of deionized water were added to 5.0 g of field moist soil in a 50 ml centrifuge tube. Dinitrogen gas was added to the headspace, the tubes sealed, and incubated at 25 °C for 14 days to allow for microbial conversion of mineralizable nitrogen to ammonium without subsequent formation of nitrate. After the incubation period, 10 ml of 4 M KCl was added to each tube, the contents shaken for 30 min, and the extracts were then filtered through Whatman 42 ash free filter paper on a vacuum extraction manifold. Ammonium was analyzed as described above and expressed on a soil dry weight basis. The initial concentration of ammonium was subtracted from this value to yield an estimate of PMN. Soil samples that were dried were later analyzed for total C and N by dry combustion (Fissions EA 1100, Milan Italy), exchangeable alkaline metals (Ca⁺², Mg⁺², K⁺, and Na⁺), and pH in a 2:1, 0.01 M CaCl₂ to soil suspension. The C/N ratio was determined from this data by dividing the total amount of C by the total amount of N. Alkaline metals were extracted by placing 10 g of air dried soil in 50 ml of 1 M NH₄Cl and shaking for 30 minutes. The suspensions were then filtered through Whatman 42 filter papers and analyzed for Ca, K, Mg, and Na by inductively coupled plasma spectroscopy (Helmke and Sparks, 1996; Suarez,

1996). Soil moisture content was determined gravimetrically by drying a 30 g moist sub-sample at 105 °C for 24 hours and then reweighing the sample. Water holding capacity was determined by measuring water content of soil samples adjusted to -30 kPa by using a ceramic pressure plate.

In the fall of 2003, we returned to a subset of five of the sites to assess N mineralization and nitrification potentials. Soil samples were analyzed for nitrification potential as determined by a 28 d aerobic incubation. Briefly, paired 30 g soil samples were wet to 80% of water holding capacity at 30 kPa and one immediately extracted and analyzed for NO_3^- as described above, and the second placed in a constant temperature chamber at 25° C for 28 days at which time it was extracted and analyzed for NO_3^- as above. Moisture content was checked and adjusted weekly and 28 day net nitrification potential calculated as the amount of NO_3^- -N at time 28 d minus the NO_3^- -N concentration at time zero. The activity of nitrifying organisms was estimated using the aerated slurry method (Hart et al., 1994). Four replicates of 30 g fresh soil samples that had been sieved and stored moist at 5°C until time of use were placed into 100 ml of water amended with $(\text{NH}_4)_2\text{SO}_4$ and KH_2PO_4 in excess of microbial demands and placed on an orbital shaker to maintain adequate aeration. An aliquot of suspension was carefully removed, diluted 1:1 with 4 M KCl to create a 2 M KCl solution and to slow activity and then immediately analyzed for NO_3^- - N concentrations at 0, 1, 2, 23, and 24 hrs. The slope of the line for the change in NO_3^- concentrations was determined and used as an estimate of nitrifier activity reported in $\mu\text{g g}^{-1} \text{hr}^{-1}$. Ammonium and NO_3^- concentrations were measured on soil extracts and slurry supernatants. The extracts and supernatants were analyzed for NH_4^+ -N and NO_3^- -N on a segmented flow analyzer (Auto Analyzer III, Bran Luebbe, Chicago, IL). The salicilate-nitroprusside method was employed for NH_4^+ and the cadmium reduction method for NO_3^- analysis (Mulvaney, 1996).

Statistical analyses

For vegetation analyses, each sampled stand was assigned to be either fire maintained or fire excluded (Table 1). Fire excluded stands were those not burned for at least 84 years (burned no later than 1919) and fire maintained stands were those that had experienced at least two fires (up to 4 at the Moose Creek site) during this period (Table 1). With the exception of the 2 fire stand in 23 Mile, where the last fire occurred in 1934, the last fire in the remaining of the fire maintained stands occurred between 1979 and 1992. Results did not change when the 2-fire stand from the 23 M site was excluded from the analysis. Such distinction between two main fire history categories allowed us to use a complete block design with no replication ANOVA with sites as blocks and fire regime as treatment. For each site and fire regime, data from a total of 3 to 6 plots were averaged (depending on whether only one or two stands were available for each fire regime). ANOVA was conducted on weighed average values to account for the difference in plot numbers for each average.

Forest floor and mineral soil properties were compared on a site by site basis between the stand not burned for at least 120 years (excluded) and the corresponding paired stand burned at the highest frequency (two or more times; maintained) and using data for each of the three plots per stand as replicates. Overall averages for fire excluded and fire maintained stands were also calculated and differences tested with paired t-tests using the excluded and maintained values per sites as paired data. We did not pool stands burned only once in the fire excluded category as for vegetation analyses as to prevent potential biases due to the presence of active charcoal in stands burned once. Whenever necessary, data were transformed to conform to the assumptions of ANOVA. When transformed data did not conform to assumptions of ANOVA a Kruskal-

Wallace test was used in place of ANOVA and a Mann-Whitney U test was employed in the place of t-tests. All data were analyzed by using SPSS version 10.0 for windows or SAS 8.2 Data were considered significant at $\alpha < 0.1$.

Results and Discussion

Physiographic and Vegetation Characteristics

While there was variation in elevation, aspect and slope among the sampled stands (Table 1) on average elevation, aspect (transformed to a linear scale) and slope in fire excluded stands were not statistically different from that in fire maintained stands. Therefore, differences in vegetation and soil characteristics between fire maintained and fire excluded stands reported below are not due to significant differences in physiographic characteristics. Aspect and elevation, however, varied between sites. Bullion Ridge was distinct from the other sites due to its north-eastern exposure (Table 1). The greatest elevation difference was between 23 Mile (the lowest site) to MacKay Bar (the highest site; Table 1; Figure 2). Slope was similar in all sites.

Interestingly, all our stands (from those subjected to no fires to those subjected to three or more fires) had a significant living old growth component. These results suggest that in these wilderness areas none of our stands had experienced stand replacing fires. More studies are necessary to corroborate whether the proportion of stand replacing fires in wilderness areas is lower than outside wilderness areas (which are generally more managed and disturbed and lack an old growth component).

Stand-level basal area by species and their total did not differ between fire maintained and fire excluded stands (Figure 3). This is most likely due to the large contribution to basal area by the old growth component, which was similar between the two fire regimes (Figure 4). In second growth forests and other old growth forests outside wilderness areas, significant increases in basal area due to the incursion of shade tolerant species (mainly Douglas-fir) have been documented (e.g. Arno et al. 1995; 1997; MacKenzie et al. *in press*). While basal area did not differ between fire excluded and fire maintained stands, total stand density was significantly higher in fire excluded stands (Figure 3). Such increase was due to a significant increase of the more shade tolerant Douglas-fir and a tendency for higher grand fir density in fire excluded relative to fire maintained stands. Diameter class distributions (Figure 4) indicate that higher tree density in fire excluded stands is mainly due to an increase in recruitment of shade tolerant species (Douglas-fir and grand fir). Note, however, that seedling density was not significantly higher in fire excluded stands than in fire maintained due to large variability. Increase in fire sensitive, shade tolerant species in fire excluded ponderosa pine systems of the interior northwest is one of the most common responses to the lack of fire (Arno et al. 1995). However, the increase in stand density in fire excluded stands reported here is much lower than that reported in unmanaged old growth stands from outside wilderness areas (Arno et al. 1995). While more data is necessary, these results suggest that recruitment of shade tolerant species in ponderosa pine forests of wilderness areas is lower than that in similar unmanaged forests but outside wilderness areas (perhaps due to seed import from adjacent managed forests). Whether disturbance associated with forest management increases recruitment and forest density to a much greater extent than in less managed areas has profound management implications and deserves future research.

Consistent with previous studies in the southwestern US (Covington and Moore 1994; Covington et al. 1997), we found a slight, but significant increase in the grass component of the understory in fire maintained stands relative to fire excluded stands (Figure 5). Although the difference is very small, it could contribute to overall changes in litter quality and nitrogen cycling (Kaye and Hart 1998; see below). Conversely, we did not find significant differences in deciduous, ericaceous and non-ericaceous shrub cover between the two fire regimes. This is in

contrast with the significant increase in total shrub cover that MacKenzie et al. (*in press*) found in ponderosa pine forests as time since last fire increased.

Soil Characteristics

As expected, increased tree density in fire excluded stands resulted in significantly greater forest soil depth relative to fire maintained stands (Figure 6). McKenzie et al. (*in press*) also showed increased forest floor depth as time since fire increased in western Montana ponderosa pine forests. While total C content of forest floor did not differ from fire maintained to fire excluded stands, total N content was significantly greater in fire excluded stands (Figure 6). Several factors could contribute to greater total N content in the litter of fire excluded stands. First, a decrease in litter quality in fire excluded stands due to the increase in shade tolerant species (mainly Douglas-fir) with longer lived foliage relative to ponderosa pine could result in an increase in non labile N bound up in complex leaf phenolic compounds (Aerts and Chapin 2000). This is explanation would be consistent with results from McKenzie et al. (*in press*) in ponderosa pine forests showing significant increases in total phenolic compounds in the forest floor with increases in time since the last fire. Second, decreased microbial activity in the forest floor of fire excluded stands could result in a relative accumulation of nitrogen in the litter. Our results for net nitrification and nitrifier activity in the mineral soil (see below) are consistent with decreased microbial activity in fire excluded relative to fire maintained stands. Alkaline metal concentration in the soil did not differ significantly between fire excluded and fire maintained stands (Table 2). This is in contrast findings from other parts of the US (Neary et al., 1999), but may relate to the immature nature of our soils and the relatively sufficient alkaline metal concentrations across all of the sites. Although, pH was significantly greater in fire maintained than in fire excluded stands the difference was too small to be of any biological significance.

Total C content and extractable nitrate and ammonium in the mineral soil (i.e. pool sizes) did not differ between fire maintained and excluded stands (Table 3). The lack of differences in nitrate and ammonium pool sizes is not surprising as pool sizes are extremely variable over time (Monleon et al. 1997, Wright and Hart 1997) and may be smaller than the fluxes themselves (Stark and Hart 1997). However, total N content and PMN were significantly higher in fire excluded stands relative to fire maintained stands (Table 3). This is consistent with earlier work from the inland Northwest showing that mineralizable N may be reduced by the reintroduction of fire (Monleon et al., 1998; DeLuca and Zouhar, 2000; Newland and DeLuca, 2000; Choromanska and DeLuca, 2001) and suggesting that a natural fire interval would likely reduce the total amount of labile N on site. While net ammonification analyses using a 28 day laboratory aerobic incubation (Figure 7) showed no differences in net mineralization between fire maintained and fire excluded stands, net nitrification (Figure 8) and nitrifier activity (Figure 9) were both significantly higher in stands exposed to two or more fires relative to stands with no fire. This suggests that in spite of lower PMN and total N in fire maintained stands, the actual pool subject to net mineralization increases in stands subjected to repeated fires. Apparently, net nitrification is not substrate limited in these systems (Schimel and Bennet 2004), but rather is being dictated by available C or the presence of inhibitory compounds (e.g. White, 1994). Further research is needed to determine whether labile C and presence of inhibitory compounds differ between fire maintained and fire excluded stands. Our results suggest that available inorganic nitrogen in the form of nitrate may increase in stands subjected to repeated fire. This appears to contrast with previous work suggesting reductions in net N mineralization and available N in Southwestern ponderosa pine forests subjected to repeated fire (Wright and Hart,

1998). However, results are difficult to compare because the system studied by Wright and Hart (1998) had been excluded from fire prior to repeated prescribed fire applications in a much higher frequency (every 2 years) than the mean fire return interval in our study. However, current research suggests that longer mean fire return intervals in ponderosa pine systems (and similar to the ones in this study) were not uncommon (Brown et al. 1999; Veblen et al. 2000). To our knowledge, this is the first study reporting higher net nitrification and nitrifier activity in natural ponderosa pine fire maintained stands compared to fire excluded stands and supports the hypothesis that fire exclusion leads to decreases in inorganic nitrogen availability.

Literature Cited

- Aerts, R. and F.S. Chapin (2000) The mineral nutrition of wild plants revisited: A re-evaluation on processes and patterns. In: A. H. Fitter and D. G. Raffaelli (eds) *Advances in Ecological Research* 30: 1-67. Academic Press.
- Anderson, L., C.E. Carlson and R.H. Wakimoto (1987) Forest fire frequency and western spruce budworm outbreaks in western Montana. *Forest Ecology and Management* 22:251-260.
- Arno, S.F. (1988) Fire ecology and its management implications in ponderosa pine forests. *In* *Ponderosa pine: the species and its management*. Eds. D.M. Baumgartner and J.E. Lotan. Symposium proceedings. Sept 29-Oct 1, 1987. Spokane, WA. Pullman, WA. Washington State University Coop Extension Publ. pp 133-140.
- Arno, S.F., M.G.Harrington, C.E. Fiedler and C.E. Carlson (1995) Restoring fire-dependent ponderosa pine forests in western Montana. *Restoration & Management Notes* 13: 32-36.
- Arno, S.F., H.Y. Smith, and M.A. Krebs (1997) Old growth Ponderosa pine and Western larch of Pre-1900 fires and fire exclusion INT-RP-495. Intermountain Research Station, Forest service, USDA, Missoula, MT.
- Brown P.M., Kaufmann M.R and W.D. Shepperd (1999) Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecology* 14:513-532.
- Choromanska, U. and T.H. DeLuca. (2001) Prescribed fire alters the effect of wildfire on soil biochemical properties in a ponderosa pine forest. *Soil Science Society of America Journal*.65:232-238.
- Covington, W.W. and M.M. Moore (1994). Southwestern ponderosa pine forest structure and resource conditions: changes since Euro-American settlement. *Journal of Forestry* 92(1): 39-47.
- Covington, W.W. and S.S. Sackett (1984) The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *Forest Science* 30: 183-192.
- Covington, W.W. and S.S. Sackett (1986) Effect of periodic burning on soil nitrogen concentration in ponderosa pine. *Soil Science Society of America Journal* 50: 452-457.
- Covington, W.W. and S.S. Sackett (1992) Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *Forest Ecology and Management* 54: 175-191.
- Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett, and M.R. Wagner (1997) Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry* 95(4): 23-29.

DeLuca, T.H. and K.L. Zouhar (2000) Effect of selection cutting and prescribed fire on N dynamics in ponderosa pine forests. *Forest Ecology and Management* 138:263-271.

Feeney, S. R., T. E. Kolb, W.W. Covington, and M.R. Wagner (1998). Influence of thinning and burning restoration treatments on presettlement ponderosa pine at the Gus Pearson Natural Area. *Canadian Journal of Forest Research* 28: 1295-1306.

Fischer, W.C. and A.F. Bradley (1987) Fire ecology of western Montana forest habitat types. USDA Forest Service. Gen. Tech. Rep. INT-90.

Fulé, P.Z., W.W. Covington, M.M. Moore (1997) Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications* 7(3): 895-908.

Hart, S.C., T.H. DeLuca, G.S. Newman, M.D. MacKenzie, and S.I. Boyle. (*in press*) Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *Forest Ecology and Management*

Helmke, PA and Sparks, D L 1996 Lithium, sodium, potassium, rubidium, and cesium. In *Methods of Soil Analysis: Part 3 - Chemical Methods*. SSSA-Book Series 5. Ed. D L Sparks. pp 551-574. American. Society of Agronomy, Madison, WI.

Hunt, H.W., E.R. Ingham, D.C. Coleman, E.T. Elliott and C.P.P. Reid (1988) Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. *Ecology* 69: 1009-1016.

Kaye, J.P. and S.C. Hart (1998) Ecological restoration alters nitrogen transformations in a ponderosa pine-bunchgrass ecosystem. *Ecological Applications* 8: 1052-1060.

Keane R.E., K.C. Ryan and S.W. Running (1996) Simulating the effects of fire on northern Rocky Mountain landscapes with the ecological process model FIRE-BGC. *Tree Physiology* 16:319-331.

Keane R.E., S.F. Arno and J.K. Brown (1989) Simulating cumulative fire effects in ponderosa pine Douglas-fir forests. *Ecology* 71:189-203.

Keeney, D.R. (1982) Nitrogen availability indices. In: Page A.L, R.H. Miller and D.R Keeney (eds). *Methods of soil analysis. Part 2: American Society of Agronomy. Madison. Wisconsin*. Pp 711-733.

MacKenzie, D.M., T.H. DeLuca, and A. Sala. (*In press*) Forest structure and organic matter analysis along a fire chronosequence in the low elevation forests of western Montana. *Forest Ecology and Management*.

Mandzak, J.M., Moore, J.A. (1994) The role of nutrition in the health of inland western forests. *Journal of Sustainable Forestry* 2:191-210

- Martin, R.E. (1982) Fire history and its role in succession. Forest Succession and stand development research in the northwest. Symp. Porc. Oregon State University, Forest Research Laboratory. Corvallis. OR.
- McLean, E.O. ed. (1982) Soil pH and lime requirement. 2nd edition. American Society of Agronomy. Soil Society of America. Madison. Wisconsin.
- Monleon, V.J., K. Chromack and J.D. Landsberg (1997) Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. Can. J. For. Res. 27:369-378.
- Mulvaney, R.S. (1996) Nitrogen – inorganic forms. Pp. 1123-1184. In: Methods of soil analysis. Part 3 – Chemical methods. D.L. Sparks (ed.). SSSA Book Series 5. Soil Sci. Soc. Am., Madison, WI.
- Neary, D.G., C.C. Klopatek, L.F. DeBano and P.F. Folliott (1999) Fire effects on belowground sustainability: a review and synthesis. For. Ecol. Manage. 122:51-71.
- Newland, J. and T.H. DeLuca (2000) Influence of fire on native nitrogen fixing plants and the soil N status of ponderosa pine forests in western Montana. Canadian Journal of Forest Research 30:274-282.
- Schimel, J.P. and J. Bennett (2004) Nitrogen mineralization: Challenges of a changing paradigm. Ecology 85: 591-602.
- Stark, J. M. and S. C. Hart. (1997) High rates of nitrification and nitrate turnover in undisturbed coniferous forests. Nature 385:61-64
- Stokes, M.A. and J.H. Dieterich (eds) (1980) Proceedings of the fire history workshop. USDA Forest Service, Gen. Tech. Rep. RM-81. 142 p.
- Stone, J.E., T.E. Kolb, et al. (1999) Effects of restoration thinning on presettlement Pinus ponderosa in northern Arizona. Restoration Ecology 7(2): 172-182.
- Suarez, D.L. (1996) Beryllium, magnesium, calcium, strontium, and barium. In Methods of Soil Analysis-Part 3 Chemical Methods. Ed. D L Sparks. pp 575-602. SSSA Book Series 5. American Society of Agronomy, Madison, WI.
- Van Hooser, D.D. and C.C. Keegan III (1988) Distribution and volumes of ponderosa pine forests. In: D.M. Baumgartner and J.E. Lotan (eds). Ponderosa pine: the species and its management; Symposium Proceedings Sept 29-Oct. 1, 1987. Spokane, WA. Pullman WA. Washington State University Coop Extension Publ. Pp:1-6.
- Veblen T.T, T. Kitzberger and J. Donnegan (2000) Climatic and human influences of fire regimes in ponderosa pine forests in the Colorado Front Range. Ecological Applications 10: 1178-1195

Wagle, R.F. and J.H. Kitchen (1972) Influence of fire on soil nutrients in a ponderosa pine type. Ecology 53:118-125.

Wallin, K.F., T.E. Kolb, K.R. Skov, and M.R. Wagner (2004) Seven-year results of thinning and burning restoration treatments on old growth ponderosa pines at the Gus Pearson Natural Area. Restoration Ecology 12:239-247.

Weber, U.M. and F.H. Schweingruber (1995) A dendrochronological reconstruction of western spruce budworm outbreaks (*Choristoneura occidentalis*) in the Front Range, Colorado, from 1720 to 1986. Trees 9:204-213.

White, C.S (1994) Monoterpenes - their effects on ecosystem nutrient cycling. J. Chem Ecol 20: 1381-1406.

Wright, R.J. and S.C. Hart (1997) Nitrogen and phosphorous status in a ponderosa pine forest after 20 years of interval burning. Ecoscience 4:526-533.

Table 1. Sites and stands sampled, number of fires, and mean elevation, aspect and slope per stand (n = 3). FE and FM indicate the category (fire excluded and fire maintained) assigned to each stand for statistical analyses. Dates of each fire in each stand are also indicated.

Site	Stand	Mean Aspect (deg)	Mean Elev. (ft)	Mean Slope (deg)	Fire Regime	Year 1st Burn	Year 2nd Burn	Year 3rd Burn	Year 4th Burn
23 Mile	0	88.7	2640	32.7	FE				
(TW)	1	122.7	2730	36.3	FE	1910			
	2	128.0	2770	38.7	FM	1910	1934		
	3	134.7	2851	33.3	FM	1910	1934	1992	
Mackay Bar	1	236.0	5947	27.3	FE	1919			
(MB)	3	250.7	5040	32.7	FM	1919	1960	1987	
Whitewater Ranch	0	220.0	4215	30.0	FE				
(WW)	1	206.7	3370	25.0	FE	1919			
	3	93.3	3113	35.0	FM	1919	1933	1988	
Lake Como	0	304.7	5091	21.0	FE				
(LC)	2	273.3	5174	35.0	FM	1924	1988		
Bullion Ridge	1	61.3	5464	37.3	FE	1914			
(BR)	3	49.3	4802	29.3	FM	1914	1944	1992	
Moose Creek	0	270.0	3141	33.3	FE				
(MC)	1	116.7	4193	25.0	FE	1910			
	4	258.0	3003	42.3	FM	1910	1934	1981	1987
Ditch Creek	0	166.0	2823	17.3	FE				
(DC)	1	124.0	3192	28.3	FE	1919			
	2	202.7	3071	23.3	FM	1919	1979		

Table 2. Exchangeable alkaline metal concentrations (mg kg^{-1}) and soil pH in stands exposed to 0 or 2 or more fires over the past 120 years in wilderness areas of western Montana and northern Idaho. The number in parentheses represents the $\pm$ one standard error of the mean ($n = 3$ for individual sites and $n = 7$ for mean).

Site	History	Ca	Mg	K	pH
23 Mile	0 Burn	240 (16)	21 (2)	31 (4)	4.3 (0.3)
	3 Burn	239 (30)	19 (2.8)	39 (8)	4.8 (0.3)
Whitewater	0 Burn	261 (15)	32 (5.8)	46 (7)	5.0 (0.2)
	3 Burn	222 (16)	22 (2.2)*	39 (8)	5.2 (0.2)
Mackay Bar	0 Burn	826 (230)	120 (33)	268 (69)	4.8 (0.2)
	3 Burn	257 (33) *	28 (5)*	62 (13) *	5.2 (0.1)*
Como Lake	0 Burn	476 (182)	35 (14)	87 (29)	4.8 (0.2)
	2 Burn	460 (227)	49 (32)	147 (111)	4.9 (0.3)
Bullion Ridge	0 Burn	303 (42)	25 (4.3)	76 (16)	4.5 (0.3)
	2 Burn	1,008 (107)*	132 (16)*	246 (40) *	4.5 (0.2)
Ditch Creek	0 Burn	278 (18)	26 (4)	41 (9)	4.8 (0.2)
	2 Burn	358 (57)	33 (7)	50 (6)	4.9 (0.3)
Moose Creek	0 Burn	400 (228)	49 (30)	76 (34)	4.4 (0.4)
	4 Burn	201 (26)	16 (3.2)	33 (6)	5.0 (0.2)
Mean	0 Burn	387 (38)	42 (24)	85 (51)	4.6 (0.1)
	2⁺Burn	386 (41)	46 (27)	84 (52)	4.9 (0.2)*

*, ** represents values from the zero burn or multiple burn are significantly different at $P < 0.05$ or 0.01 respectively as determined using a Mann-Whitney U test.

Table 3. Soil N status in stands exposed to 0 or 2 or more fires over the past 120 years in wilderness sites of western Montana and northern Idaho.

Site	History	Total N	PMN	NO ₃ ⁻ -N	NH ₄ ⁺ -N
23 Mile	0 Burn	8.4 (1.8)	23.1 (5.8)	0.15 (0.02)	2.08 (0.58)
	3 Burn	7.1 (0.6)	13.4 (4.6)	0.24 (0.04)	2.68 (1.70)
Whitewater	0 Burn	5.8 (1.5)	10.9 (3.4)	0.15 (0.00)	0.99 (0.17)
	3 Burn	7.1 (2.3)	9.3 (2.0)	0.15 (0.00)	0.76 (0.14)
Mackay Bar	0 Burn	9.2 (1.8)	24.5 (4.9)	0.23 (0.09)	0.90 (0.17)
	3 Burn	3.7 (1.2) **	23.9 (4.8)	0.55 (0.22) *	0.74 (0.20)
Como Lake	0 Burn	12.1 (3.4)	56.7 (29.4)	0.23 (0.01)	2.90 (0.86)
	2 Burn	7.1 (1.3)*	11.1 (4.5)*	0.20 (0.01)	0.84 (0.24)*
Bullion Ridge	0 Burn	9.9 (2.0)	25.6 (6.1)	0.23 (0.00)	1.36 (0.40)
	2 Burn	4.7 (1.4)**	18.6 (3.7)	0.32 (0.18)	1.11 (0.34)
Ditch Creek	0 Burn	8.4 (1.8)	15.0 (6.6)	0.20 (0.08)	0.69 (0.30)
	2 Burn	8.0 (1.9)	22.0 (5.2)	0.20 (0.06)	0.84 (0.18)
Moose Creek	0 Burn	6.0 (1.2)	22.8 (6.4)	0.20 (0.09)	1.27 (0.36)
	4 Burn	4.7 (0.8)	11.8 (4.0)*	0.15 (0.00)	0.93 (0.22)
Mean	0 Burn	8.7 (1.4)	25.3 (2.2)	0.20 (0.03)	1.47 (0.14)
	2⁺ Burn	5.5 (1.0)*	17.2 (3.6)*	0.26 (0.08)	1.25 (0.09)

*, ** represents values from the zero burn or multiple burn are significantly different at P < 0.05 or 0.01 respectively as determined using a Mann-Whitney U test.

Figure Legends

Figure 1. Study area and location of sampling sites.

Figure 2. Average aspect (linear transformation), elevation, and slope in fire maintained and fire excluded stands. There were no statistically significant differences between fire excluded and fire maintained for any of the variables.

Figure 3. Average stand basal area, tree density (> 5 cm DBH), and seedling and sapling density (< 5 cm diameter at base) per species and total values in fire excluded and fire maintained stands. Within each column different letters denote significant differences between fire excluded and fire maintained stands ($P < 0.1$).

Figure 4. Size class distribution by species in fire maintained and fire excluded stands.

Figure 5. Average grass and forb frequency (upper panel) and deciduous, ericaceous and non-ericaceous evergreen shrubs (lower panel) in fire excluded and fire maintained stands. Within each column different letters denote significant differences between fire excluded and fire maintained stands ($P < 0.1$).

Figure 6. Total N and C content (%) in the forest floor and forest floor depth in fire excluded and fire maintained stands.

Figure 7. Net ammonification rates in the mineral soil from 28 day aerobic incubations in stands that had not experienced fire in the past 120 years (control) versus paired stands that had experienced two or more fires during the same period (burned). The overall average is also shown. Net ammonification rates were not significantly different between control (excluded from fire) and burned (two or more fires) stands.

Figure 8. Net nitrification rates in the mineral soil from 28 day aerobic incubations in stands that had not experienced fire in the past 120 years (control) versus paired stands that had experienced two or more fires during the same period (burned). The overall average is also shown. Mean net nitrification rate was significantly greater in burned (fire maintained stands) than in controls (excluded).

Figure 9. Nitrifier activity in the mineral soil from 28 day aerobic incubations in stands that had not experienced fire in the past 120 years (control) versus paired stands that had experienced two or more fires during the same period (burned). The overall average is also shown. Mean nitrifier activity was significantly greater in burned (fire maintained stands) than in controls (excluded).

Study Area and Site Locations

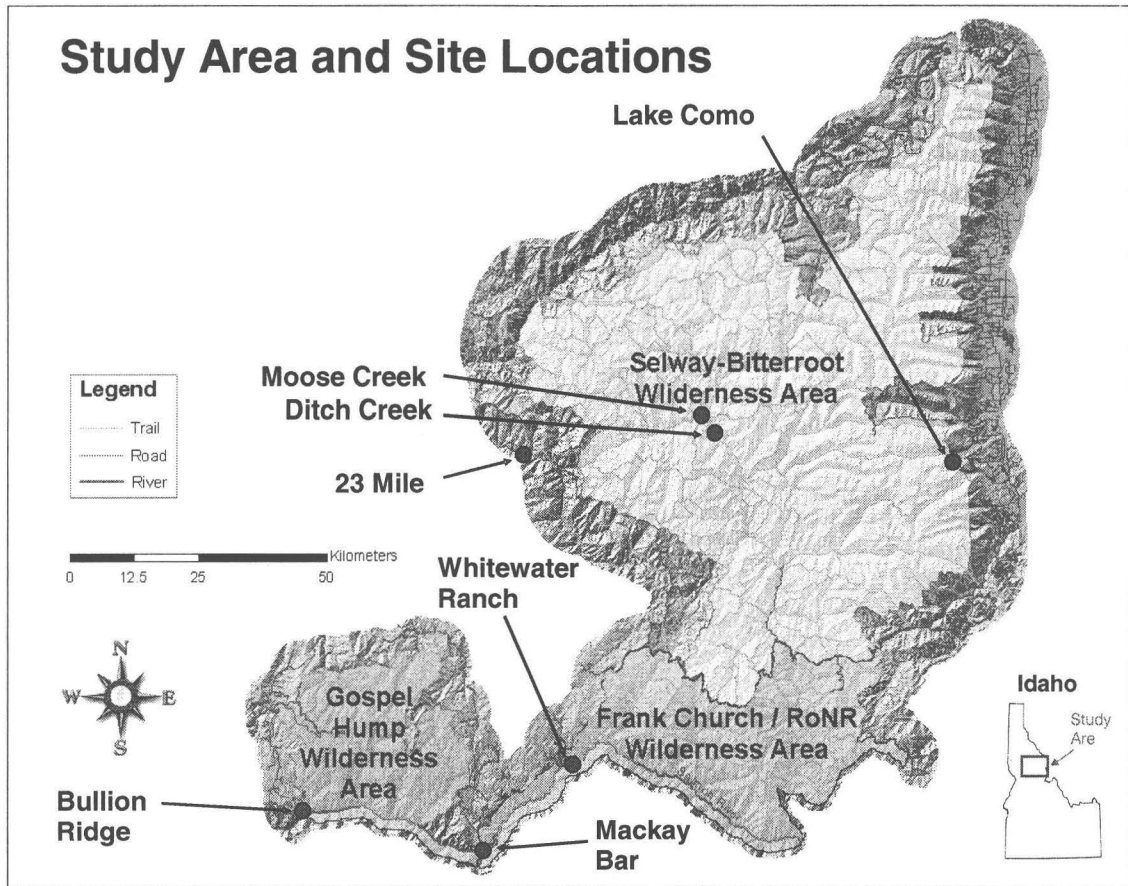


Figure 1

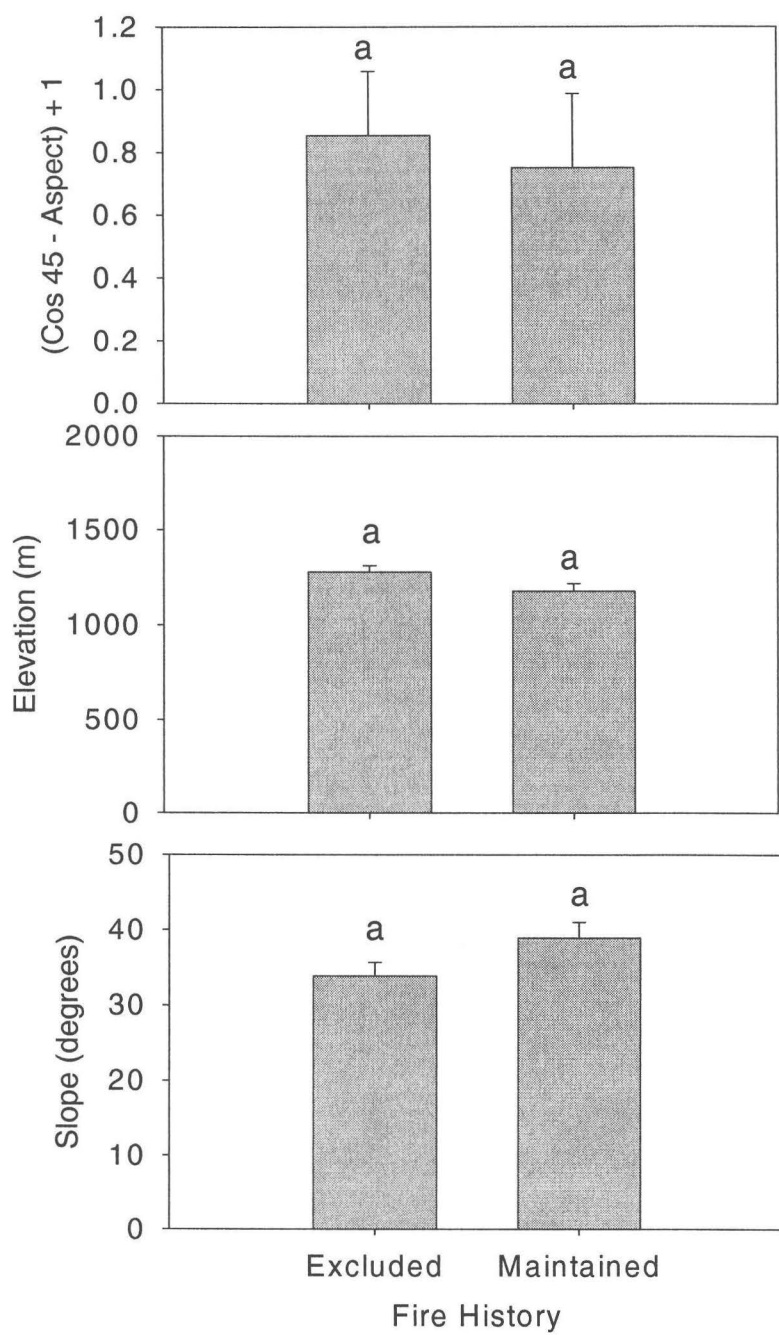


Figure 2

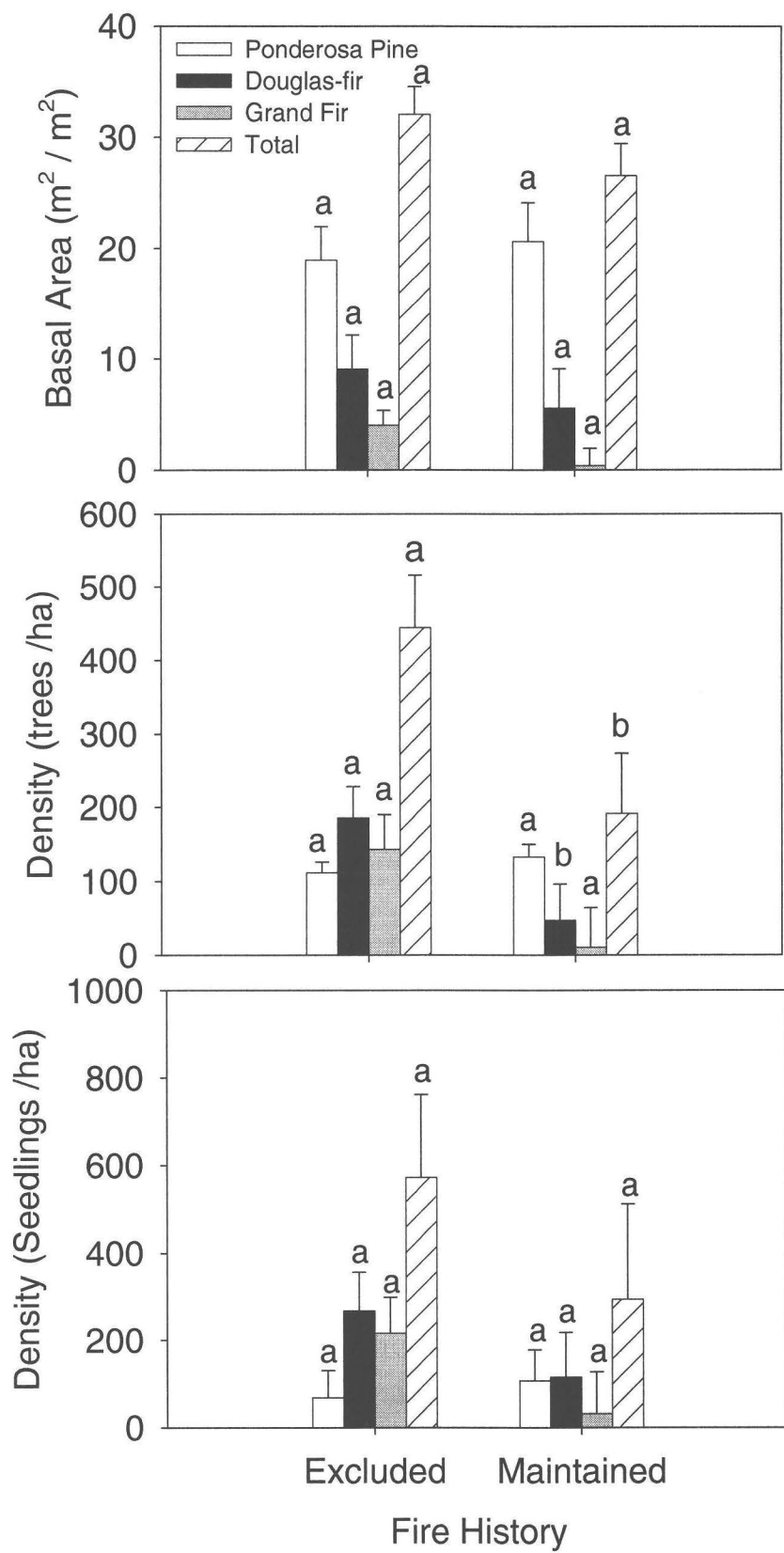


Figure 3

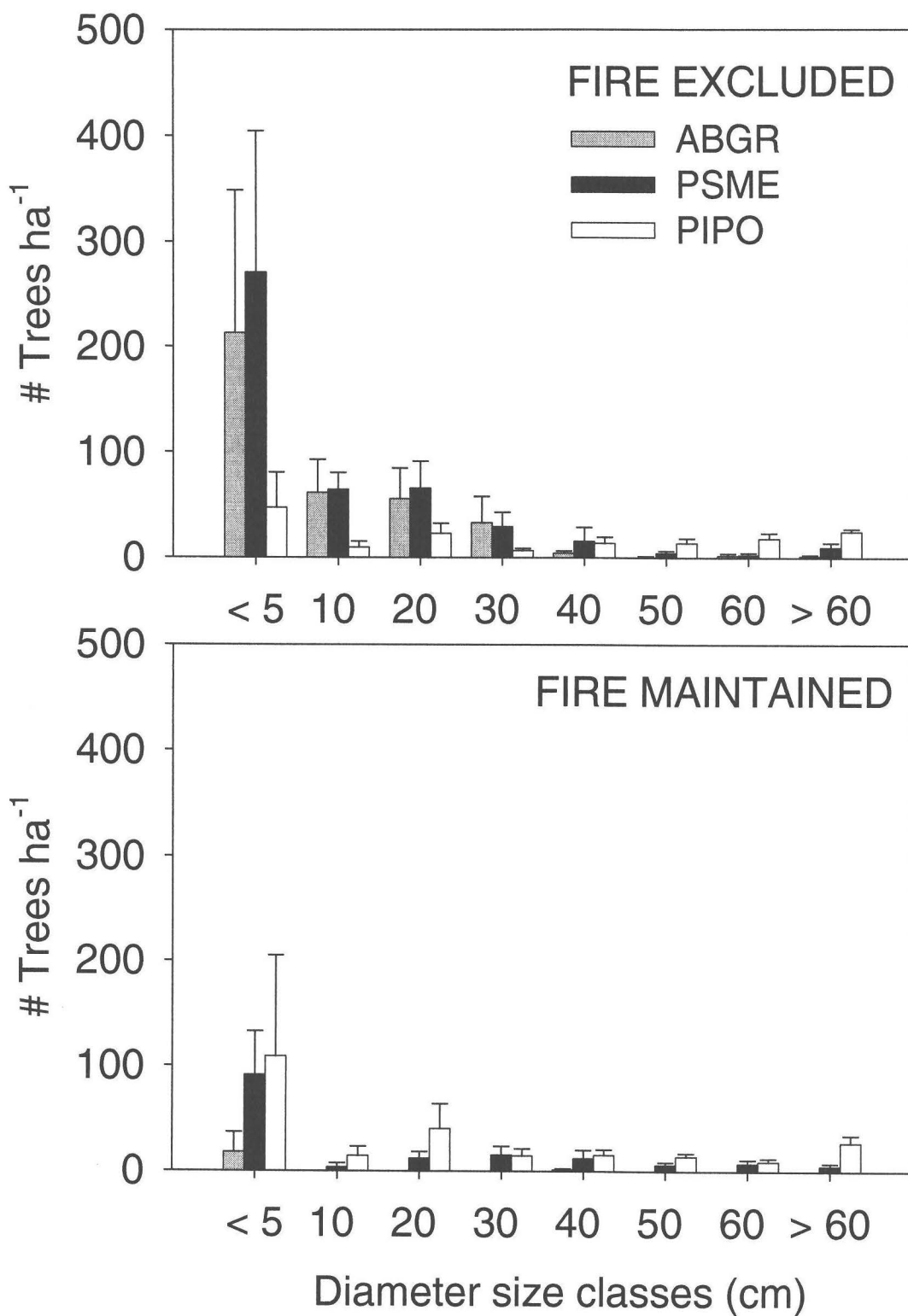


Figure 4

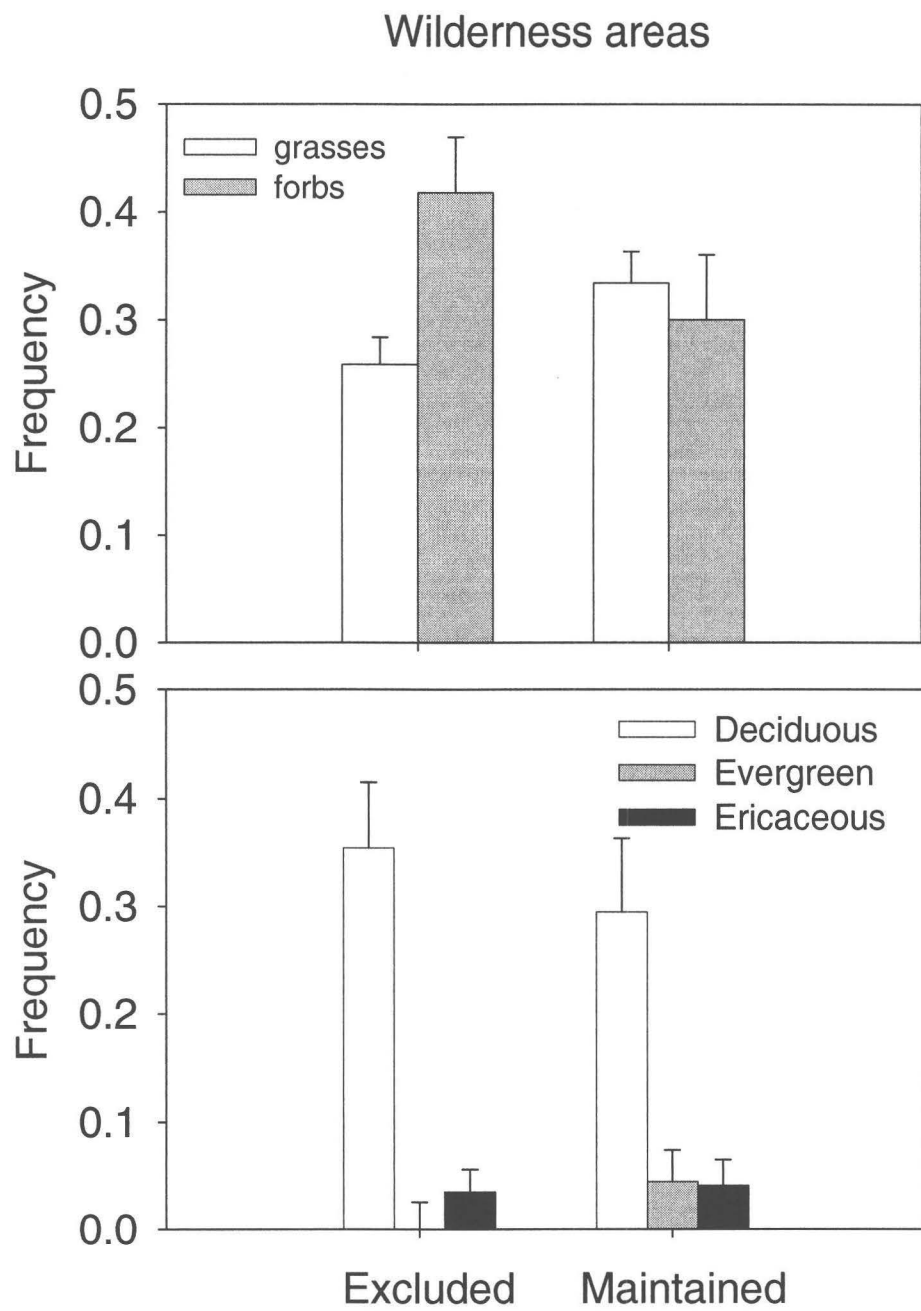


Figure 5

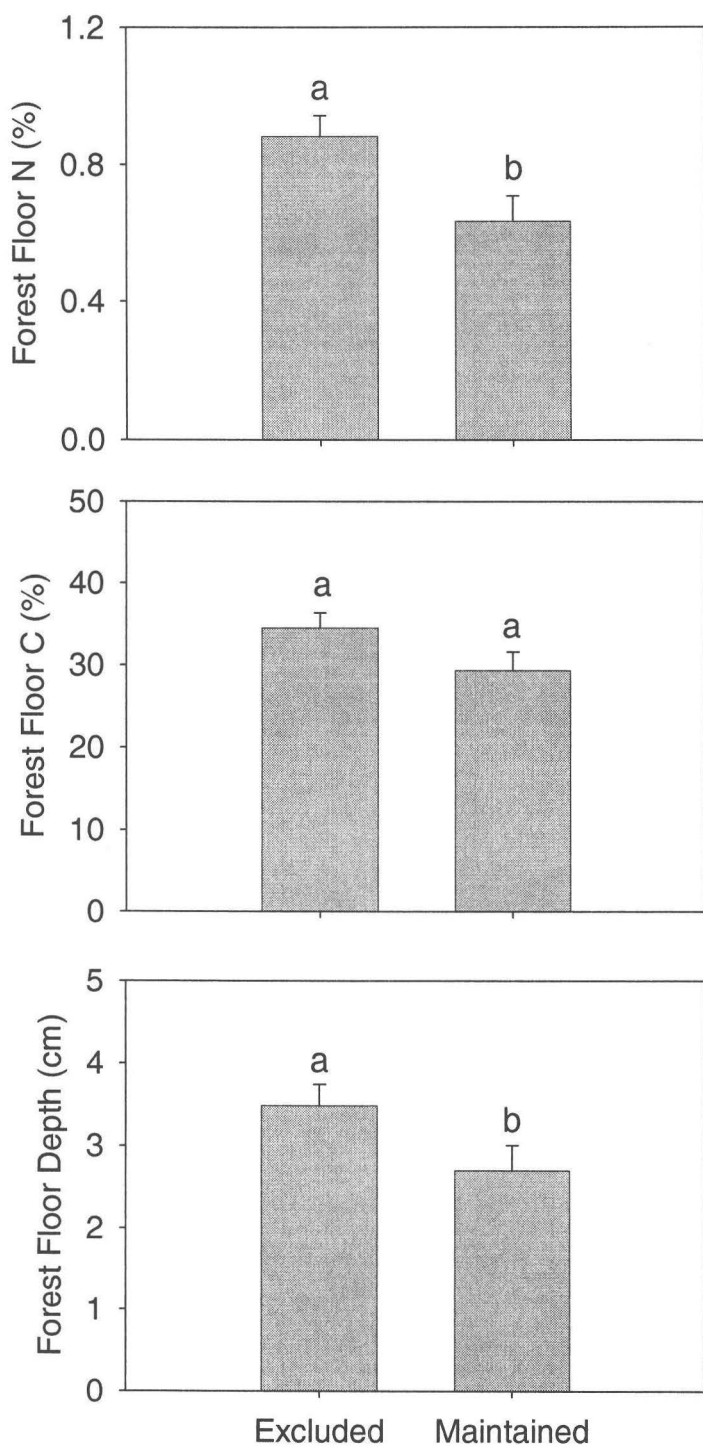


Figure 6

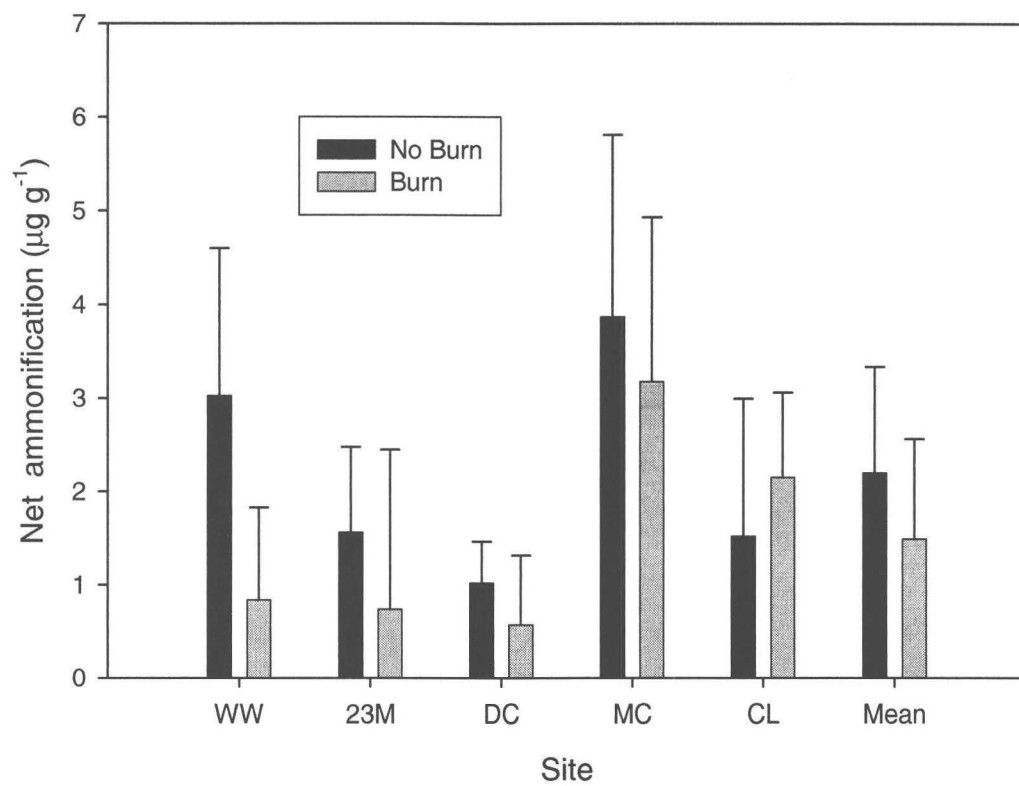


Figure 7

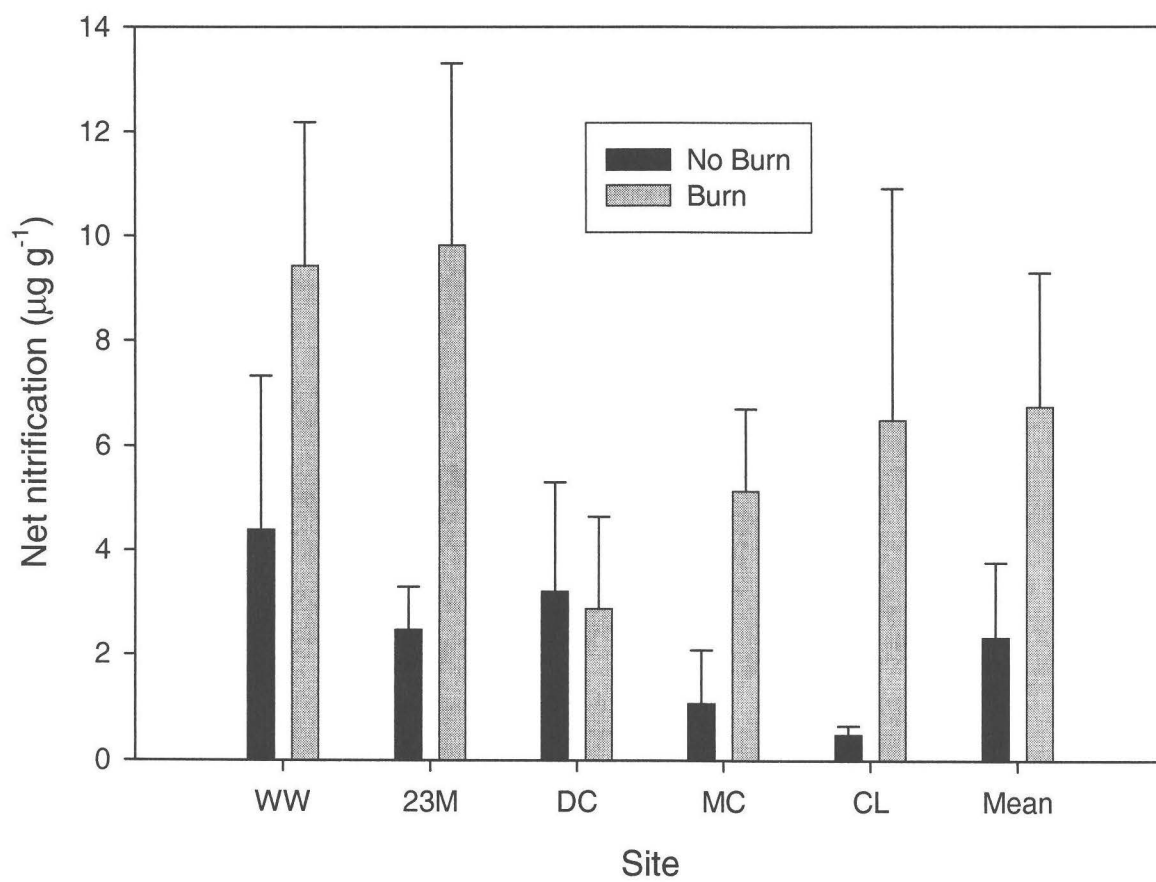


Figure 8

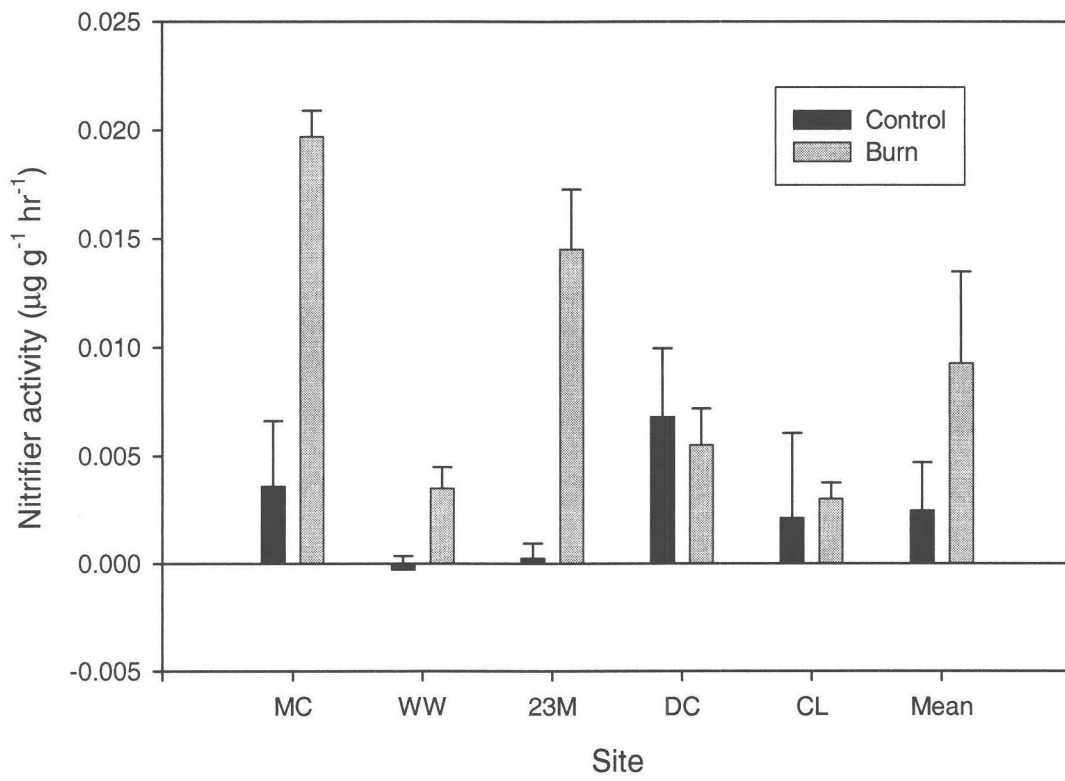


Figure 9